

Cytotaxonomy of the *Thelypteris japonica* Complex (Thelypteridaceae)

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Cytological and morphological observations were carried out for the *Thelypteris japonica* complex. Diploids ($2n = 62$) show echinate perispores, stramineous stipes, and short hairs at pinnule margins (mean, 0.1–0.2 mm long), and prefer rocky areas, usually growing on rocks. Tetraploids ($2n = 124$) have membranous perispores and long hairs at pinnule margins (0.2–0.4 mm long), and grow on forest floors. The occurrence of triploids ($2n = 93$) characterized by abortive spores is also confirmed. Two type specimens belonging to this complex were examined and compared with cytological vouchers. As a result, we regard the diploids as *T. musashiensis* (stat. nov.), the tetraploids as *T. japonica* f. *japonica* (having castaneous stipes) and f. *formosa* (stat. nov., having stramineous stipes), and the triploids as a hybrid between *T. japonica* \times *T. musashiensis*.

Key words: Chromosome number, cytotaxonomy, hybrid, ploidy, spore, *Thelypteris japonica*, *Thelypteris musashiensis*

Thelypteris sensu lato is distributed mainly in the tropics and subtropics of the world and comprises nearly 300 species (Ching 1936), of which some 37 species occur in Japan (Iwatsuki 1995). Although the taxonomy of Japanese species was compiled comprehensively in floristic works (Ito 1939, Tagawa 1959, Iwatsuki 1965, 1992, 1995, Nakaike 1975, 1982, 1992, Kurata & Nakaike 1983), detailed cytotaxonomic and cytogeographic studies have been made only for several species complexes involving aneuploidy, polyploidy or different reproductive modes (Mitui 1966, Masuyama 1979, Matsumoto 1982, Matsumoto & Yano 1989, Hirabayashi 1989, Nakato 1998, 2002, Nakato *et al.* 2002). The eastern Asian species *Thelypteris japonica* (Baker) Ching is one of such complexes that

need more detailed cytotaxonomic research.

Thelypteris japonica is a medium-sized deciduous fern distributed in Japan, Korea and China. It was originally described as *Nephrodium japonicum* Baker in 1891 from Nagasaki, Japan. Subsequently, the following four related taxa were described.

1. *Dryopteris formosa* Nakai, non Maxon 1909. Nakai (1931) described this from Korea, Prov. Keiki, Kôryô (Gyeonggi-Do, Guangneung; Nakai 13259, T1-holotype) and Prov. Keiki, Namsan (Seoul, Namsan; Uchiyama s.n., T1-paratype). It was distinguished from *Thelypteris japonica* in having stramineous stipes, slender leaves, minute and slender hairs on the indusia and pinnae, glabrous midribs of the pinna-segments, and fewer (9–11) cells of the sporangial annulus. The spore mor-

phology was described to have "exosporium angulato-elevati-reticulatum".

2. *Thelypteris japonica* var. *glabrata* Ching. Ching (1936) described this variety from Querpaert Isl. (Jeju Isl.), Korea (type: *Faurie* 27, pro parte, herbarium uncertain¹⁾). This variety was distinguished from var. *japonica* in having stramineous stipes, glabrous indusia and abaxial surface of leaves, and crenate-denticulate margins of pinnules. Ching (1936) described that two varieties, var. *japonica* and var. *glabrata*, are intermingled in *Faurie* 27, and the type of var. *glabrata* is too meager. Iwatsuki (1965) noted that *Faurie* 27 deposited in KYO is var. *japonica* and both varieties occur mixed in nature, and *Faurie* 26 (from Quelpaert Isl.) in KYO is var. *glabrata*.

3. *Thelypteris japonica* f. *viridescens* H. Ito. Ito (1939) recognized two varieties in *Thelypteris japonica*, var. *typica* and var. *glabrata* (syn. *Dryopteris formosa* Nakai), and he further divided the former variety into two formas, f. *vulgaris* and f. *viridescens*, the latter of which was proposed earlier but semiillegitimately as a variety by Makino (1933). Forma *vulgaris* is identical to *T. japonica* var. *japonica* in the sense of the current taxonomy. Ito (1939) described f. *viridescens* briefly as: "Laminae ovate-oblongae, tenuiores, stipitibus viridescens", but did not cite type specimen nor any other authentic specimen.

4. *Thelypteris japonica* var. *musashiensis* Hiyama. Hiyama (1951) described this variety from Mt. Bôno-ore at the boundary between Tokyo and Saitama Prefectures, Japan (type: *Hiyama s.n.*, July 27, 1948, TNS). Hiyama distinguished it from f. *viridescens* by diagnostic characters such as the more sparsely hairy leaves, glabrous abaxial side of the rachis, and glabrous indusia. He also pointed out that this variety prefers growing on rocks.

All of the above four taxa are characterized by the stramineous stipes and other characters, and distinguished from var. *japonica* having castaneous stipes. However, the taxonomy of the taxa has

been controversial even in recent floristic studies. Iwatsuki (1965, 1992, 1995) and Shing *et al.* (1999) recognized three varieties in this complex; var. *glabrata* (syn. *Dryopteris formosa* Nakai), var. *musashiensis* (syn. f. *viridescens*), and var. *japonica*. Nakaike (1975, 1982, 1992) and Kurata & Nakaike (1983) recognized var. *formosa* (syn. var. *glabrata*, and var. *musashiensis*), f. *viridescens*, and var. *japonica*.

Cytologically, a diploid ($n = 31$) was reported by Mitui (1967, 1968) in var. *musashiensis*²⁾. Triploids and tetraploids were reported in var. *japonica* by Kurita (1963), Mitui (1968, 1980) and Kuri-zono (1987). The data suggest that the *Thelypteris japonica* complex is cytologically complicated probably involving polyploidization and hybridization, and further that the morphological variation is correlated to the cytological one. However, in no previous study both morphology and cytology of the *T. japonica* complex has ever been examined in detail.

In this study we examined cytotypes of materials collected mainly in Tokyo Prefecture. We also made a comparative morphological examination of the type specimens of *Dryopteris formosa* and *Thelypteris japonica* var. *musashiensis*, and cytological voucher specimens. Based on data obtained, we propose a revised taxonomic account of the *T. japonica* complex.

Materials and Methods

The localities of materials are listed in Table 1, together with the results of chromosome counts and morphological examinations. The method for somatic chromosome observations is the same as the one described in Nakato (1998), and voucher specimens are deposited in TI. Spores from the vouchers and the type specimens were mounted in Bioleite (Ohken Co., Tokyo) and the length along the long axis of bilateral spores, excluding perispores, was measured for 50 samples per specimen using an ocular micrometer by light microscopy. For scan-

TABLE 1. Localities of materials used in this study, and morphological characters examined of the *Thelypteris japonica* complex. A: Specimen number collected by N. Nakato. B: Altitude (m). C: Substratum of habitat (t.soil, thin layered soil on rock; s.wall, stone wall; r.soil, rocky soil with gravel). D: Ornamentation of spore (ech, dense echinate; mem, membranous; abo, abortive). E: Color of stipe (str, stramineous; cas, castaneous). F: Hairiness of indusia (the mean number of hairs / indusium: +, less than 30; ++, 31-60; +++, more than 61). G: Hairiness of the abaxial side of rachis (–, absent; +, present only in basal part of rachis; ++, present nearly along the length of rachis). H: Length of hairs at pinnule margin (mm, mean). Boxes indicate uniform features of cytotypes.

Ploidy, chromosome number								
Locality	A	B	C	D	E	F	G	H
Diploid, $2n = 62 \rightarrow$ <i>Thelypteris musashiensis</i>								
O-tanba, near Mt. Bohno-ore, Tokyo	2545 ^{a)}	440	rock	ech	str	+	–	0.17
ibid.	2547 ^{a)}	440	rock	ech	str	+	–	0.18
Atagoyama, Okutama-machi, Tokyo	2523 ^{a)}	430	t.soil	ech	str	+	–	0.13
ibid.	2524 ^{a,b)}	440	s.wall	ech	str	+	–	0.13
Nokogiri-one, Okutama-machi, Tokyo	2535 ^{a,c)}	700	r.soil	ech	str	+++	–	0.10
ibid.	2529 ^{a,b,c)}	710	rock	ech	str	+	–	0.20
ibid.	2530 ^{a)}	710	rock	ech	str	+	–	0.17
ibid.	2532 ^{a,c)}	710	rock	ech	str	+	–	0.20
ibid.	2533 ^{a,c)}	710	rock	ech	str	+	–	0.14
Tetraploid, $2n = 124 \rightarrow$ <i>T. japonica</i>								
Anazawa, Naguri-mura, Saitama	2466 ^{a,b,c)}	320	soil	mem	cas	++	++	0.24
ibid.	2467 ^{a,c)}	320	soil	mem	cas	++	++	0.29
Zoushiki, Higashiyamato-shi, Tokyo	2537 ^{b)}	100	soil	• ^{d)}	str	•	–	0.24
Narahashi, Higashiyamato-shi, Tokyo	2506 ^{a,c)}	100	soil	mem	str	+	–	0.20
ibid.	2536 ^{a)}	120	soil	mem	cas	+++	++	0.36
ibid.	2498 ^{b)}	120	soil	•	cas	•	++	0.32
ibid.	2499	120	soil	•	cas	•	++	0.28
Umegaya-toge, Ome-shi, Tokyo	2507 ^{a,c)}	250	soil	mem	cas	+++	++	0.37
ibid.	2508	250	soil	•	cas	•	++	0.40
ibid.	2509 ^{b,c)}	250	soil	•	cas	++	++	0.25
Tokura, Akiruno-shi, Tokyo	2513 ^{a)}	200	soil	mem	cas	++	++	0.36
ibid.	2514 ^{a,b,c)}	210	soil	mem	cas	++	++	0.36
Motosyuku, Hinohara-mura, Tokyo	2510	340	soil	•	cas	++	++	0.37
ibid.	2515 ^{a)}	340	soil	mem	str	•	++	0.37
O-tanba, Okutama-machi, Tokyo	2503 ^{a,c)}	300	soil	mem	cas	+++	++	0.23
ibid.	2504 ^{c)}	300	soil	•	cas	++	++	0.21
ibid.	2505 ^{b)}	300	soil	•	cas	•	++	0.33
Atagoyama, Okutama-machi, Tokyo	2518 ^{a)}	400	soil	mem	cas	++	++	0.36
Triploid, $2n = 93 \rightarrow$ <i>T. japonica</i> × <i>T. musashiensis</i>								
Ishihata, Mizuho-machi, Tokyo	2093	170	soil	•	str	•	–	0.29
Atagoyama, Okutama-machi, Tokyo	2519	400	soil	abo	cas	++	+	0.32
ibid.	2522	430	soil	•	cas	+	+	0.35
ibid.	2526	440	soil	abo	str	++	+	0.23
ibid.	2525	440	s.wall	abo	str	++	–	0.19
Nokogiri-one, Okutama-machi, Tokyo	2534 ^{b)}	700	r.soil	abo	cas	+++	+	0.26

a) Specimens examined for spore length, and the number of annulus cells of sporangium (except for nos. 2513 and 2515).

b) Approximate chromosome counts ($2n =$ ca. 62, ca. 124 or ca. 93).

c) Specimens examined for the number of spores per sporangium.

d) Material was not available.

ning electron microscopic (SEM) observations, spores were put on the specimen stub covered with the duplex Scotch tape, spattered with gold, and observed using Akashi MSN-4 SEM at 10 kV. Spore ornamentations were also examined from herbarium specimens with stramineous stipes deposited in KYO, MAK, TI, TKB and TNS. Sporangia were mounted in Bioleit and the number of annulus cells was counted for 10 samples per specimen. To examine reproduction modes, the number of spores per sporangium was counted. Indusia were embedded in Bioleit, and the number of hairs per indusium was counted for 5-10 samples of each voucher, and 3-4 samples from the types. The length of hairs at the pinnule margin was measured using an ocular micrometer for 20 samples per cytological voucher specimen, and 10-20 samples per herbarium specimen and the type.

Results and Discussion

1. Chromosome numbers and habitats

Somatic chromosome numbers were counted in 33 materials, of which nine individuals were diploid, 18 were tetraploid, and six were triploid, based on $x = 31$, from three, eight and three localities, respectively (Table 1, Figs. 1, 2). Because the number of spores per sporangium was 50-64 in all diploids and

tetraploids examined (Table 1), the reproduction manner is suggested to be sexual in both cytotypes.

The diploids were collected from relatively high altitudes at 430-710 m in deciduous or mixed forests, while the tetraploids were from lowlands at 100-400 m in deciduous or *Cryptomeria* afforestation areas. There is a clear difference in the substratum of habitats between the diploid and the tetraploid (Table 1). The diploids grew in rocky areas, on rock surfaces, thin layered soils on rocks, rocky soils with gravels, or stone walls near cliffs, while the tetraploids grew on humus rich soils in forests.

The triploids were obtained from throughout the examined areas and grew on humus rich soils (170 m, 400-440 m alt.), stone wall (440 m alt.) or rocky soil (700 m alt.). Occasionally, triploids grew sympatrically with either diploids or tetraploids. The triploid *no.* 2519 and the tetraploid *no.* 2518 occurred at a distance of only about 1 m at the collection site at 400 m alt. of Atagoyama, and the triploid *no.* 2525 and the diploid *no.* 2524 grew together on the same stone wall at another site at 440 m alt. These observations suggest that the triploid cytotype has originated from crossing between a diploid and a tetraploid.

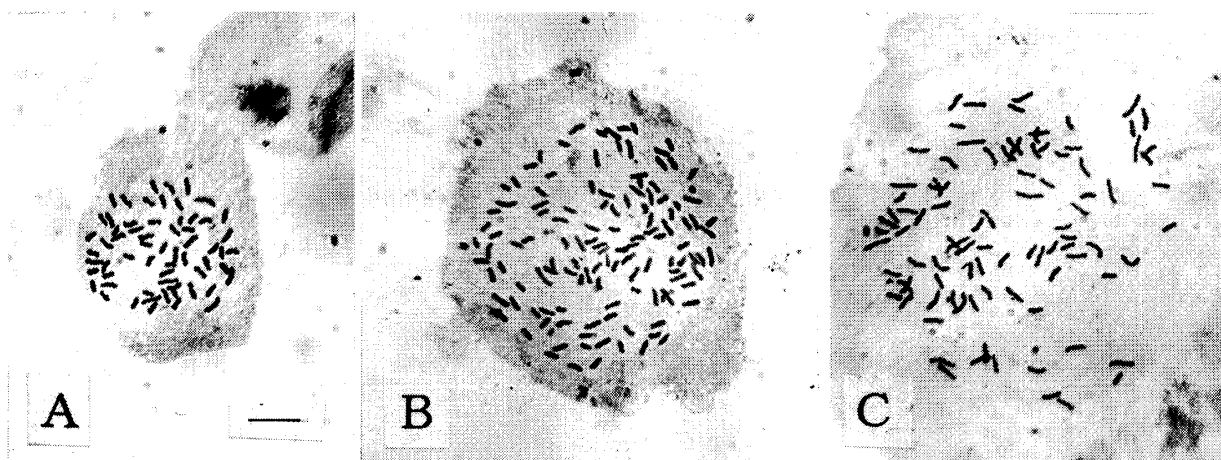


FIG. 1. Somatic chromosomes. A: Diploid, $2n = 62$; *no.* 2535. B: Tetraploid, $2n = 124$; *no.* 2513. C: Triploid, $2n = 93$; *no.* 2526. Scale bar: 10 μ m.

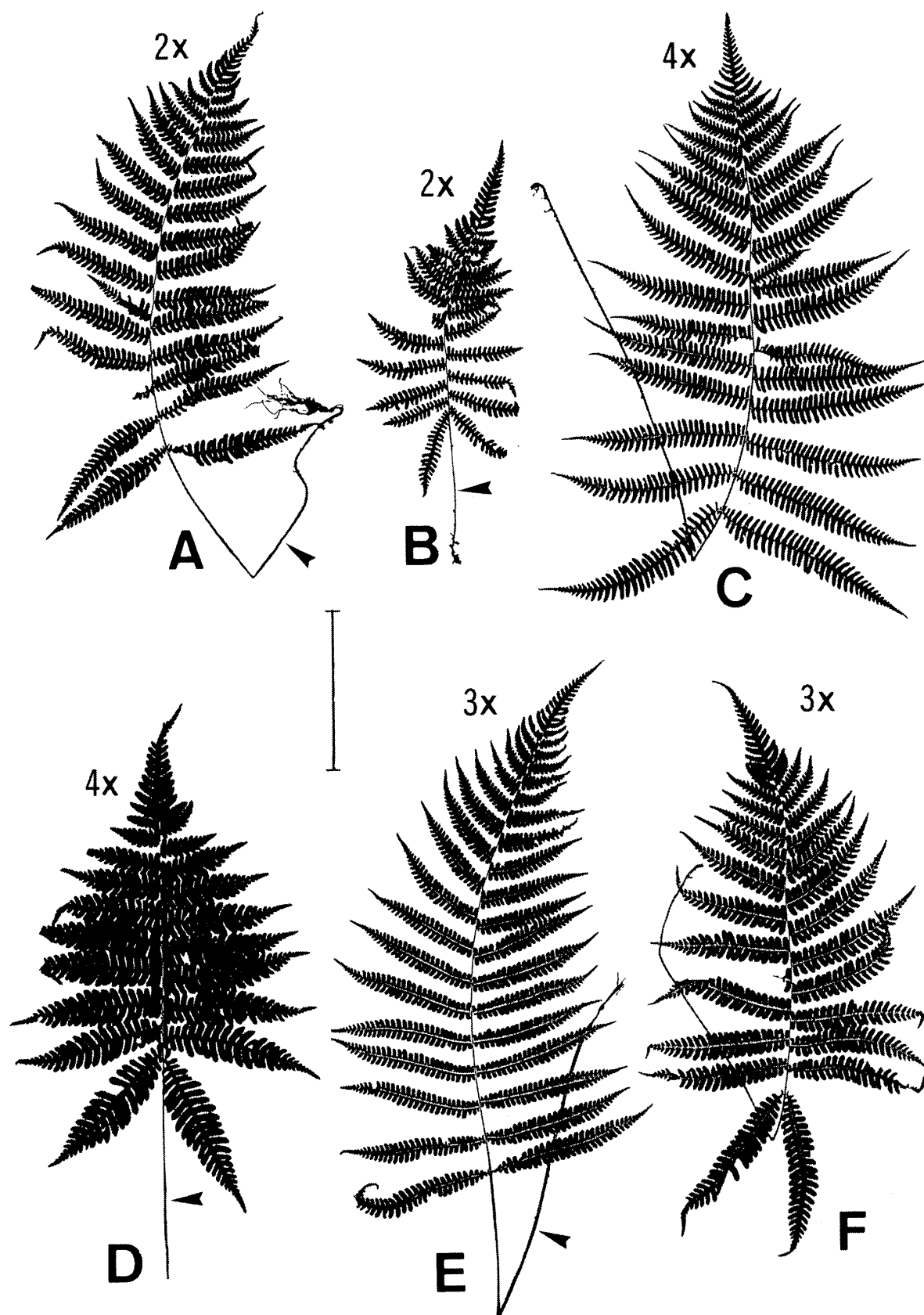


FIG. 2. Silhouettes of fertile (A-C, E, F) and sterile (D) leaves of cytological voucher specimens. A: Diploid, no. 2535. B: Diploid, no. 2533. C: Tetraploid, no. 2513. D: Tetraploid, no. 2537. E: Triploid, no. 2526. F: Triploid, no. 2522. Stipes marked by arrows are stramineous, and the others castaneous. Scale bar: 10 cm.

2. Morphology of voucher specimens

2-1. Spores and annulus cells

The diploids and the tetraploids produced normal-shaped, dark-brown, bilateral spores, while the triploids yielded abortive spores along with a few normal bilateral ones (Fig. 3). The diploids and the tetraploids are distinct in spore ornamentation. By light microscopy (LM), the spore wall of the diploids is covered by many small projections, while that of the tetraploids has continuous ridges (Fig. 3). By scanning electron microscopy (SEM), the spores of the diploids have dense, laterally fused echinae, while those from the tetraploids have prominently perforated wings forming a large reticulate pattern (Fig. 4A-D). The wall ornamentation of normal-shaped spores from the triploids consists of low wings and sparse short echinae, an intermediate character between the diploids and the tetraploids (Fig. 4 E, F). No difference exists in the length of spores between the diploids and the tetraploids; the mean (\pm SD) was $44.4 \pm 3.8 \mu\text{m}$ in the former ($N = 450$, nine specimens) and $44.7 \pm 3.2 \mu\text{m}$ ($N = 500$, 10 specimens) in the latter.

The spores of the echinate type have been illustrated in *Thelypteris japonica* var. *formosa* by Kurata & Nakaike (1983), and the membranous type in *T.* (or *Parathelypteris*) *japonica* by Ogata (1929), Ito (1939), Wood (1973), Kuramoto (1978), Mitui (1982), Kurata & Nakaike (1983), and Shin *et*

al. (1999). From the present observations, the specimen with the echinate spore wall is certainly diploid, and those with the membranous wall are tetraploid.

The number of annulus cells of sporangia was counted in the diploid and tetraploid cytotypes. In nine diploids, the range of the number was 11-18 and the mean (\pm SD) was 14.2 ± 1.7 ($N = 90$); and in eight tetraploids, the range was 10-15 and the mean (\pm SD) was 12.7 ± 1.2 ($N = 80$). The diploids had slightly more numerous cells than the tetraploids, though the variation ranges of the two cytotypes were largely overlapped.

2-2. Color of stipe

The color of the stipe was constant in every specimen (Table 1). All diploids had stramineous stipes except basal 1/5-1/3 brown portions. By contrast, the stipes of 15 tetraploid specimens were castaneous, and those of three specimens were stramineous like those of the diploids. The tetraploids with stramineous stipes were rarely found sympatrically in the populations of tetraploids with castaneous stipes. As to the triploids, three individuals had stramineous stipes, and other three had castaneous ones.

2-3. Hairiness of indusia

In three diploids, nos. 2533, 2545 and 2547, the

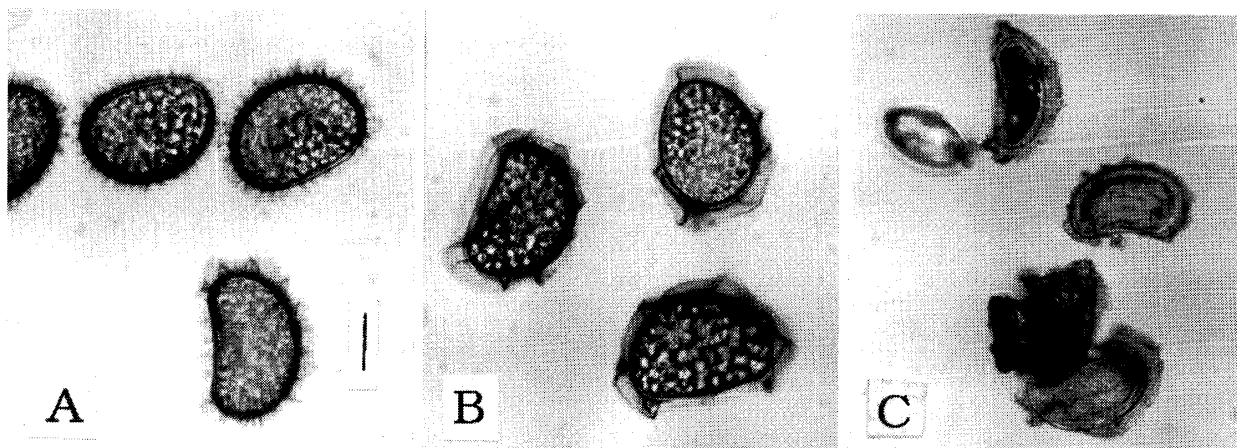


FIG. 3. LM micrographs of spores. A: Diploid, no. 2532. B: Tetraploid, no. 2503. C: Triploid, no. 2526. Scale bar: 20 μm

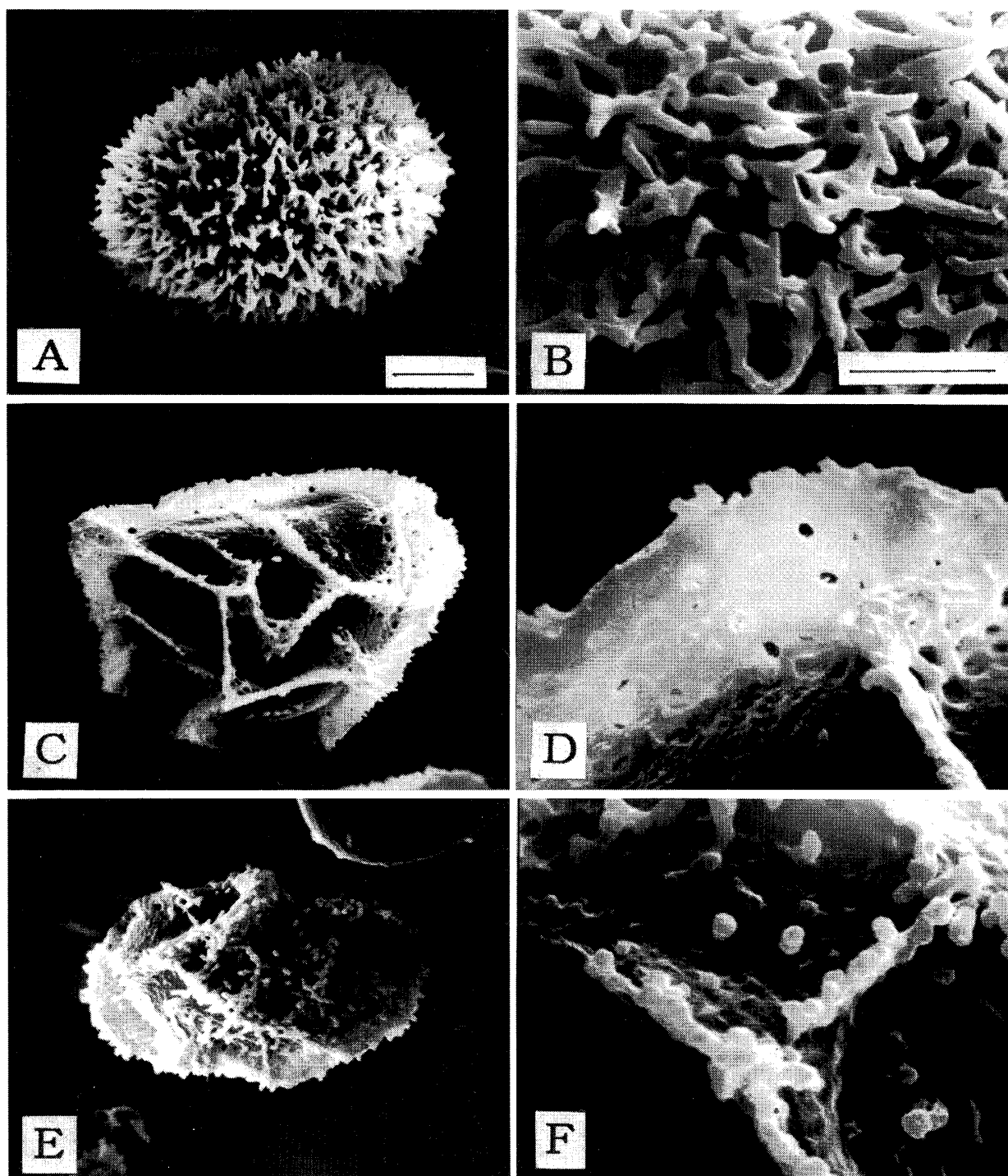


FIG. 4. SEM micrographs of spores. A & B: Diploid, no. 2532. C & D: Tetraploid, no. 2507. E & F: Triploid, no. 2526. Scale bars: 10 μ m (for A, C, E), 5 μ m (for B, D, F).

indusia were both glabrous or very sparsely pubescent (less than 10 hairs per indusium). All other diploid, tetraploid and triploid specimens had more densely pubescent indusia, though hair density was very variable according to specimens (Table 1, Fig.

5). These results show that there is no close relationship between the hairiness of indusia and the level of ploidy, though most diploids tend to have fewer hairs.

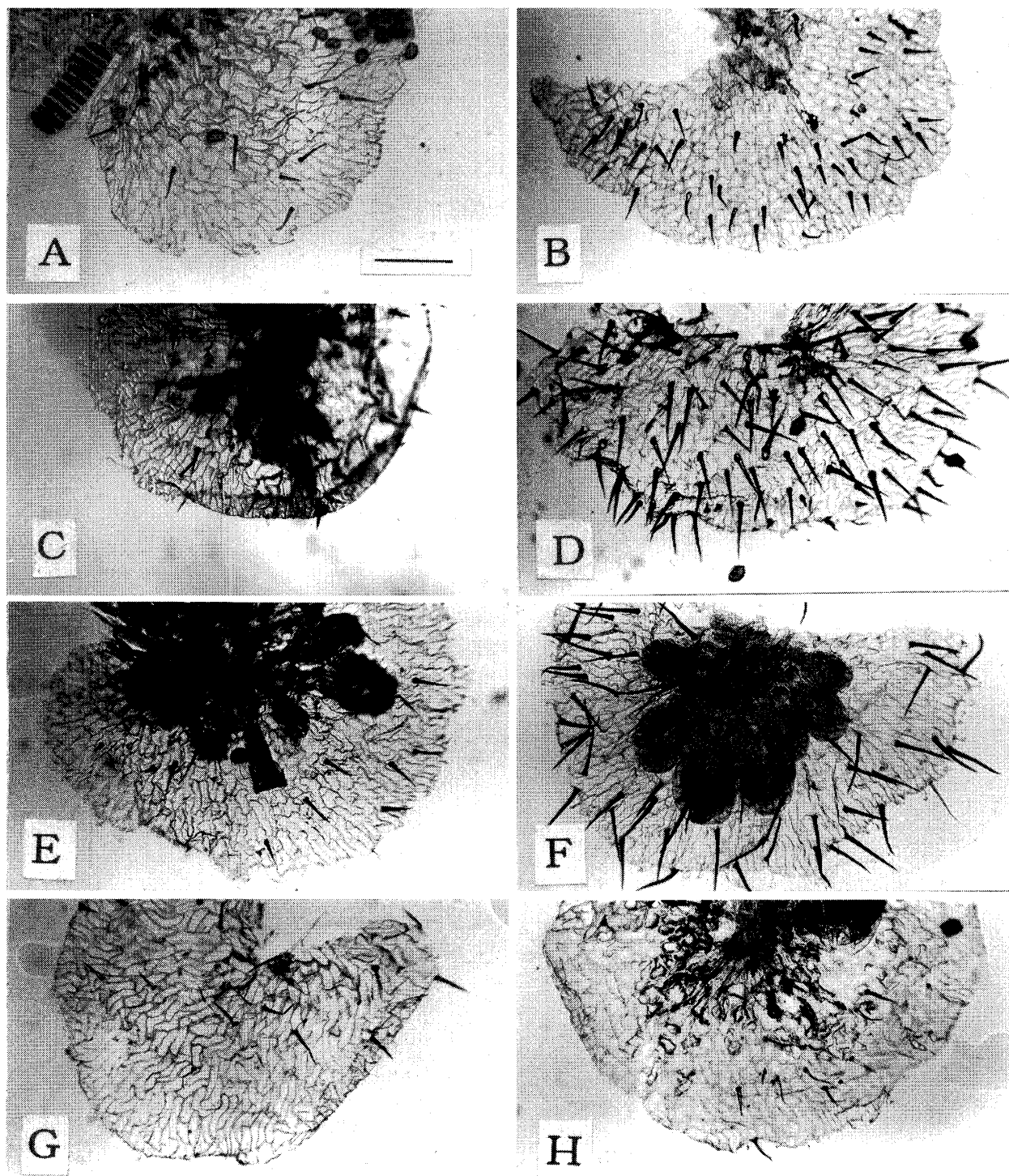


FIG. 5. Variation in hairiness of indusia. A: Diploid, no. 2524. B: Diploid, no. 2535. C: Tetraploid, no. 2506. D: Tetraploid, no. 2536. E: Triploid, no. 2522. F: Triploid, no. 2534. G: Nakai 13259 (TI), type of *Dryopteris formosa* Nakai. H: Hiyama s.n. (TNS), type of *Thelypteris japonica* var. *musashiensis* Hiyama. Scale bar: 0.2 mm.

2-4. Hairiness of rachis

The groove on the adaxial side of the rachis was covered by dense minute hairs in all voucher specimens. On the contrary, there is a difference in the hairiness on the abaxial side of the rachis (Table 1). It was entirely glabrous in all diploids, and two of 18 tetraploids also had glabrous rachises. The other 16 tetraploids had minute hairs along the length, though densities were variable according to the specimens. In the triploids, two specimens were glabrous, but four specimens were pubescent only in the basal 1/2 to 1/3 parts of the rachis.

2-5. Length of hairs at pinnule margin

All voucher specimens had minute unicellular hairs on both surfaces of leaves, though the densities were very variable according to specimens. In comparison, the length of hairs at the pinnule margins differed between the cytotypes; the hairs were shorter in the diploids (0.10–0.20 mm long) than in the tetraploids (0.20–0.40 mm), and the triploids showed similar values (0.19–0.35 mm) to those of the tetraploids (Fig. 6).

2-6. Pinna size and number of veinlet pairs

The sizes of pinnae were measured for all fertile leaves. The largest pinna (usually the lowest one) of each leaf was measured in 16 leaves of nine diploids, 16 leaves of 10 tetraploids, and seven leaves of four triploids. The mean length (\pm SD) was 7.8 ± 1.7 cm (range, 4.6–10.4 cm) in the diploids, 11.9 ± 2.2 cm (7.5–15.3 cm) in the tetraploids, and 11.0 ± 1.6 cm (9.4–14.5 cm) in the triploids. The mean width was 1.7 ± 0.4 cm (1.0–2.2 cm) in the diploids, 1.9 ± 0.3 cm (1.2–2.5 cm) in the tetraploids, and 1.8 ± 0.2 cm (1.4–2.0 cm) in the triploids. The pinna length tended to be longer in the tetraploids and the triploids than in the diploids, though the length ranges overlapped. By contrast, there was no remarkable difference in the pinna width.

The number of veinlet pairs was surveyed in

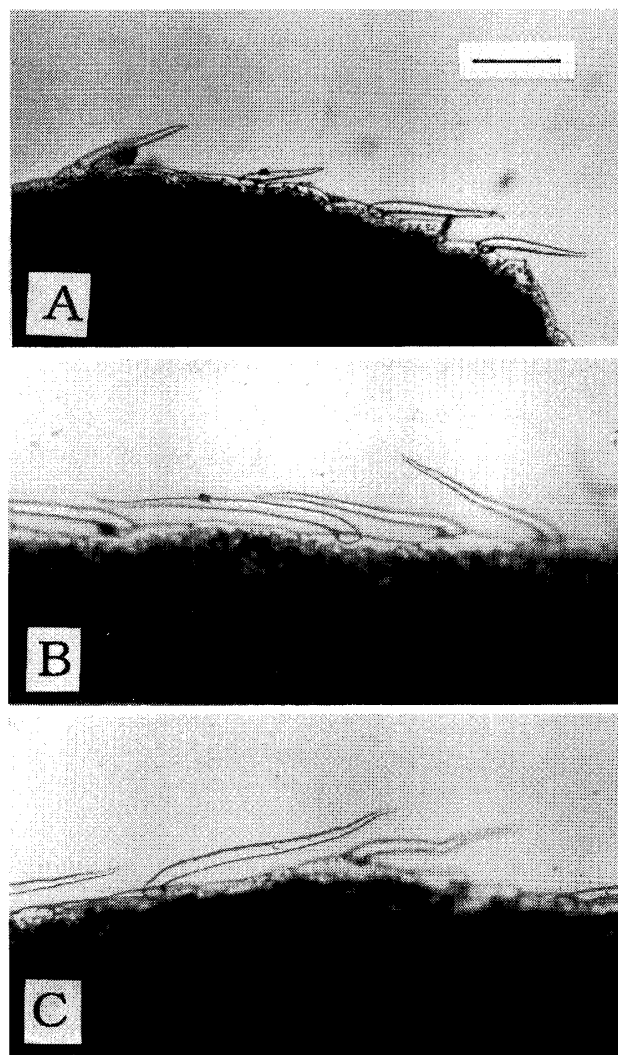


FIG. 6. Hairs at pinnule margin. A: Diploid, no. 2524. B: Tetraploid, no. 2467. C: Triploid, no. 2526. Scale bar: 0.1 mm.

middle pinnules of the largest pinnae. They were 5–9 in the diploids, 7–10 in the tetraploids, and 6–8 in the triploids. Veinlets were simple in most specimens, but rarely once forked in one diploid (no. 2529) and four tetraploids (nos. 2466, 2503, 2505, 2509).

Important characters useful to discriminate the cytotypes are summarized in Table 1. The data show that the spore morphology is the most useful diagnostic character. In addition, the habitat preference (rocky areas), the stramineous stipes and the glabrous rachis on the abaxial side are common in the diploids, and the soil on forest floors is a

preferred habitat to the tetraploids. Moreover, the hairs on the pinnule margins are shorter in the diploids (0.10-0.20 mm) than the tetraploids (0.20-0.40 mm).

3. Spores and pinna sizes of herbarium specimens with stramineous stipes

Individuals with stramineous stipes occurred throughout the three levels of ploidy (2x, 3x, 4x), while those with castaneous stipes were found only in the tetraploid and triploid cytotypes (Table 1). Then, we examined spores from specimens with stramineous stipes preserved in KYO, MAK, TI, TKB and TNS, to infer their cytotypes, i.e. echinate (2x), membranous (4x) or abortive (3x), and the results obtained are shown in Appendix. The specimens

were unambiguously divided into the three types even by LM. All three types were detected in Korean as well as Japanese specimens. Therefore, there certainly exist three ploidy levels in Korea (Fig. 7).

The sizes of pinnae were also measured for those herbarium specimens (see Appendix). The results of the measurements, included those obtained in the cytological voucher specimens, are shown in Fig. 8. The mean length (\pm SD) of the largest fertile pinna was 8.2 ± 1.9 cm (range, 3.8-12.0 cm; $N = 41$) in diploids and suspected diploids (echinate type), 10.8 ± 2.3 cm (7.3-15.3 cm; $N = 29$) in tetraploids and suspected tetraploids (membranous type), and 10.4 ± 2.1 cm (7.8-14.8 cm; $N = 14$) in triploids and suspected triploids (abortive type). The mean width was 1.7 ± 0.4 cm (range, 0.8-2.7

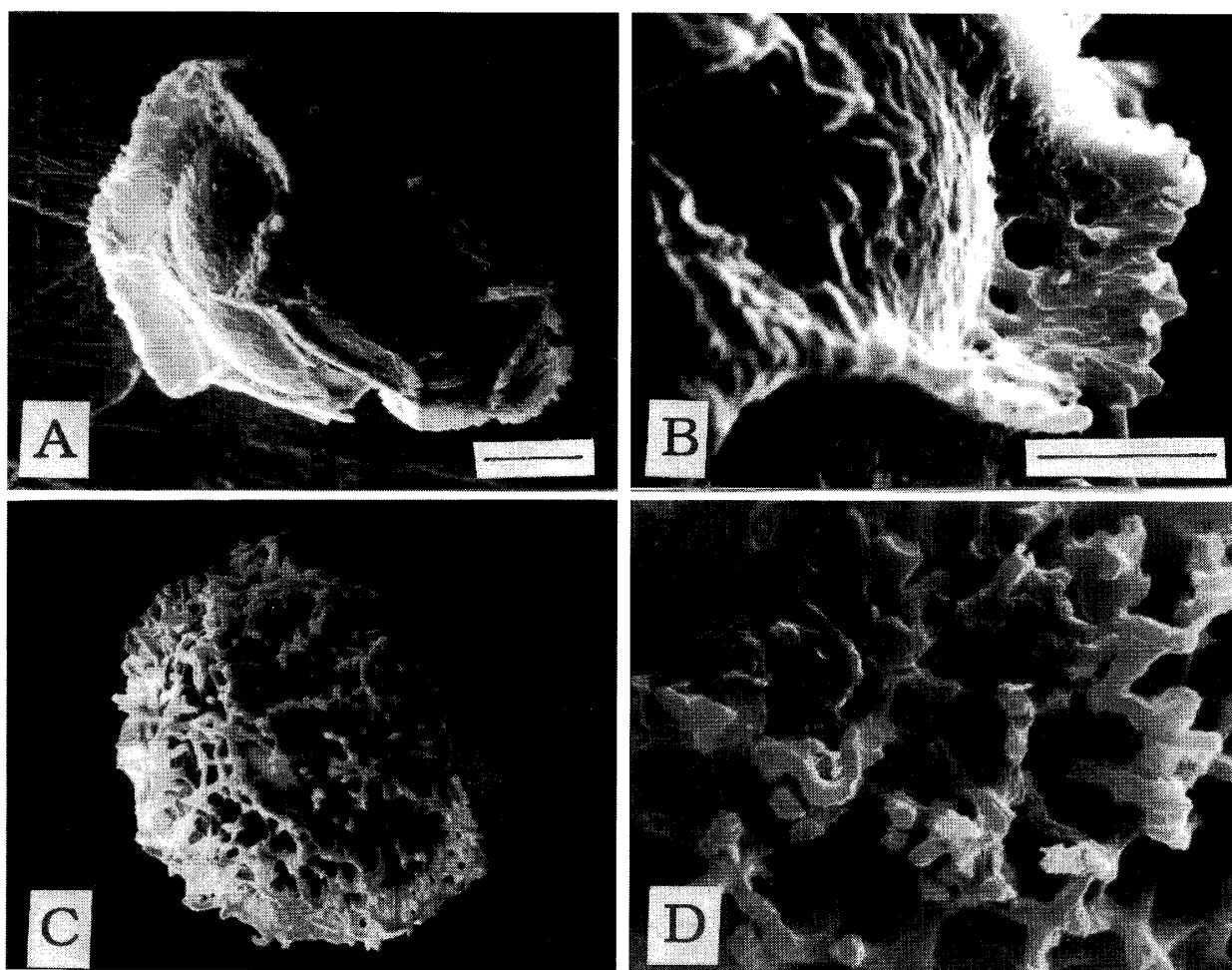


FIG. 7. SEM micrographs of spores in herbarium specimens from Korea. A & B: Nakai 13259 (TI), type of *Dryopteris formosa* Nakai, membranous type. C & D: Okamoto 19063 (TNS), echinate type. Scale bars: 10 μ m (for A, C), 5 μ m (for B, D).

cm), 1.8 ± 0.3 cm (1.1–2.5 cm), 1.8 ± 0.3 cm (1.3–2.7 cm), in the diploid, tetraploid and triploid groups, respectively. The ratio of pinna width to pinna length was 0.20 ± 0.03 (range, 0.16–0.29), 0.17 ± 0.02 (0.13–0.22), 0.17 ± 0.02 (0.12–0.21), in the diploid, tetraploid and triploid groups, respectively. Data show that the pinnae of tetraploid and triploid tend to be longer and narrower than those of the diploids, but variation ranges largely overlap.

4. Observations of type specimens

4-1. *Dryopteris formosa*

The holotype (Nakai 13259, TI) consists of one fertile leaf with many mature spores, two sterile leaves, and three stipes lacking laminae on the rhizome (Fig. 9A). Spores are membranous by LM and prominently perforated wings by SEM (Fig. 7A, B), indicating that in spore wall ornamentation the type is identical to the tetraploid voucher. The mean

length (\pm SD) of spores is 43.0 ± 2.4 μ m. The number of annulus cells is 11–13 (mean, 11.8). The stipe is stramineous, and the rachis is glabrous on the abaxial side. Indusia are pubescent, 17–20 hairs in each of three indusia examined (Fig. 5G). The hairs at the pinnule margin are 0.26 mm long (mean; $N = 20$). The largest pinna of the fertile leaf is 6.2 cm long and 1.3 cm wide, and the veinlets are 5–6-paired. Here we should pay attention to the three stipes without laminae. The stipes are all about 2.0 mm thick, and those of three leaves with laminae are 0.7–1.2 mm. Therefore, it is possible that the stipes had larger laminae than the three laminae of the type (Fig. 9A).

Nakai (1931) cited another specimen (paratype, *T. Uchiyama s.n.*, July 30, 1902, TI) in the description of *Dryopteris formosa*. The sheet consists of three young fertile leaves, from which mature spores could not be obtained. The pinnae are 4.0 cm long

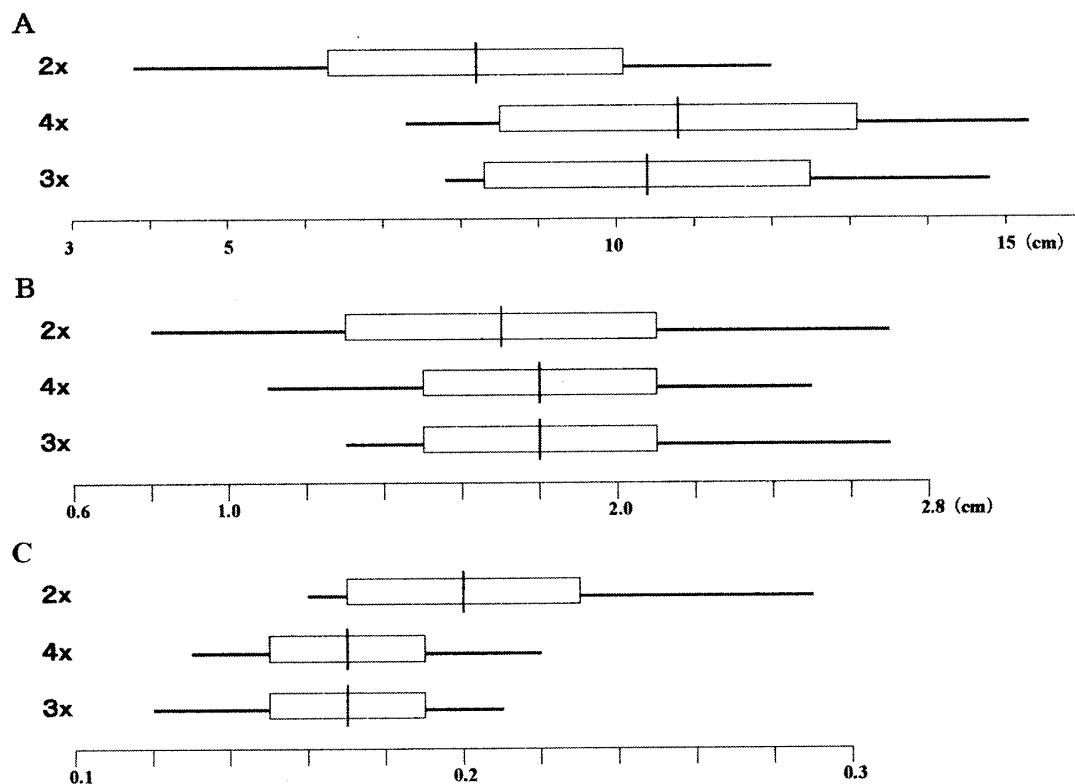


FIG. 8. Variation in pinna size and form (the largest pinna in each fertile leaf). A: Pinna length. B: Pinna width. C: Ratio of pinna width to pinna length. Ranges, standard deviations and means are shown. $N = 41$ for 2x (including 25 suspected 2x), 29 for 4x (including 13 suspected 4x) and 14 for 3x (including seven suspected 3x).

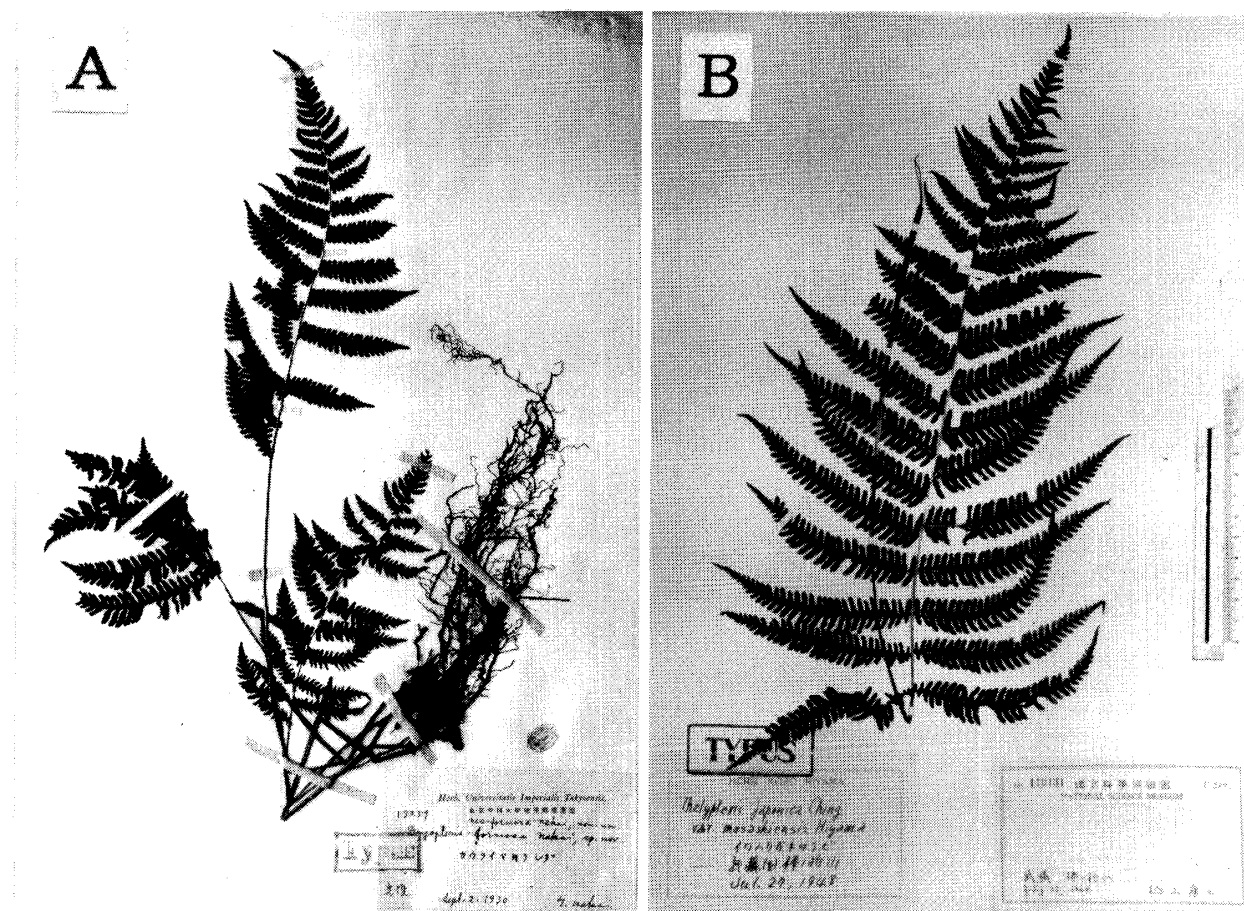


FIG. 9. Type specimens of the *Thelypteris japonica* complex. A: Nakai 13259 (TI), *Dryopteris formosa* Nakai. B: Hiyama s.n. (TNS), *Thelypteris japonica* var. *musashiensis* Hiyama. Scale bar: 10 cm.

and 1.1 cm wide, and the length of hairs at the pinule margin is 0.28 mm (mean; $N = 10$).

4-2. *Thelypteris japonica* var. *musashiensis*

The type (Hiyama s. n., July 27, 1948, TNS) has a single young fertile leaf (Fig. 9B). Many bilateral distorted spores are too young to observe their ornamentation. The number of annulus cells is 13-16 (mean, 14.2). The stipe is stramineous and the rachis is glabrous on the abaxial side. Although Hiyama (1951) mentioned that the indusia were glabrous, we confirmed 4-16 unicellular hairs per indusium (four indusia were examined; Fig. 5H). The hair length at the pinnule margin is 0.20 mm (mean; $N = 10$). The largest pinna is 10.6 cm long and 1.9 cm wide, and the veinlets are 8-9-paired.

The holotype of *Dryopteris formosa* Nakai probably is a tetraploid because of the membranous ornamentation of spores. Although the ploidy level of the paratype could not be judged due to the lack of mature spores, the hair lengths at segment margins were similar to those of the tetraploid vouchers.

The holotype of *Thelypteris japonica* var. *musashiensis* had no mature spores, from which we could not estimate its ploidy level. However, the habitat preference of var. *musashiensis* is useful. Hiyama (1951) emphasized that this variety prefers rocks. This habitat agrees well with that of the diploid vouchers and differs from that of the tetraploids growing exclusively on the soil in forests. Moreover, other characters that deviate from those of the diploid cytotype were not encountered in the type of var. *musashiensis*. Therefore, we assume

Key to taxa of the *Thelypteris japonica* complex

1. Spores normal, bilateral; diploid or tetraploid ($x = 31$)
 2. Spores with membranous perispore; rachis pubescent or rarely glabrous on abaxial side; hairs at pinnule margin 0.2-0.4 mm long (mean); stipes castaneous or rarely stramineous; plant growing on forest floor, on soil; tetraploid..... *Thelypteris japonica* (3)
 3. Stipe castaneous..... f. *japonica*
 3. Stipe stramineous f. *formosa*
 2. Spores with echinate perispore; rachis glabrous on abaxial side; hairs at pinnule margin 0.1-0.2 mm long (mean); stipe stramineous; plant growing in rocky areas, usually on rock; diploid
..... *T. musashiensis*
 1. Spores abortive, triploid..... *T. japonica* \times *T. musashiensis*

that var. *musashiensis* is diploid.

5. Taxonomy

From the above observations and discussion, we conclude that the diploid and the tetraploid differ distinctively from each other in the spore ornamentation, length of hairs at the pinnule margin, and habitat (Table 1). The differences merit separation at the species level (tetraploid *Thelypteris japonica* and diploid *T. musashiensis*). The type specimen of *T. japonica* is certainly tetraploid, because of the castaneous stipe (Baker 1891). Individuals with stramineous stipes have been referred to different taxa, i.e. *Dryopteris formosa*, *T. japonica* var. *glabrata*, f. *viridescens*, and var. *musashiensis*. The holotype of *D. formosa* Nakai is inferred as tetraploid by having membranous spores. In the only reliable specimen of var. *glabrata* (Faurie 26; Korea, Quelpaert Isl.; one sterile leaf; KYO) identified by Iwatsuki (1965), the mean hair length at the pinnule margin was 0.39 mm, which is consistent with that of the tetraploid vouchers.

As to f. (or var.) *viridescens* (Makino 1933, Ito 1939), we could not find the type specimen as well as any herbarium specimens identified by Makino and Ito as f. (or var.) *viridescens* in KYO, MAK, TI, TKB and TNS. Nonetheless, f. *viridescens* can be recognized as tetraploid, because Ito (1939)

described f. *viridescens* under var. *typica* (= var. *japonica*) with membranous reticulate spores. By contrast, var. *musashiensis* is considered to be diploid, as mentioned above. In conclusion, the *Thelypteris japonica* complex comprises two species, *T. japonica* with f. *formosa* (4x) and *T. musashiensis* (2x) (Table 2). There is a hybrid between the two. These taxa can be identified by using the following key.

1. *Thelypteris japonica* (Baker) Ching, Bull. Fan Mem. Inst. Biol. 6: 312, 1936; H.Ito, in Nakai & Honda, Nov. Fl. Jap. 4: 134, 1939; Iwatsuki, Mem. Coll. Sci. Univ. Kyoto, B, 31: 163, 1965; Fern & Fern Allies Jap. 215, 1992; in Iwatsuki *et al.* (eds.) Fl. Jap. 1: 186, 1995; Nakaike, Enum. Pterid. Jap. 299, 1975; Kurata & Nakaike, Ill. Pterid. Jap. 3: 586, 1983 – *Nephrodium japonicum* Baker, Ann. Bot. 5: 318, 1891 — *Aspidium japonicum* (Baker) Makino, Bot. Mag. Tokyo 10: 110, 1896 – *Dryopteris japonica* (Baker) C.Chr., Ind. Fil. 272, 1905 — *Lastrea japonica* (Baker) Copel., Gen. Fil. 139, 1947; Ohwi, Fl. Jap. Pterid. 98, 1957; Tagawa, Col. Ill. Jap. Pterid. 110, 1959 — *Parathelypteris japonica* (Baker) Ching, Acta Phytotax. Sin. 8: 304, 1963; Nakaike, New Fl. Jap., Rev. & enlarg. ed. 564, 1992; Shing *et al.*, Fl. Reipubl. Popularis Sin. 4: 51, 1999 — *Wagneriopteris japonica* (Baker) Á.

TABLE 2. Taxonomic treatments of the *Thelypteris japonica* complex. Synonyms are shown in parentheses.

Ito (1939)	Iwatsuki (1965, 1995) ^{a)}	Nakaike (1975) ^{b)}	Present study
T. japonica	T. japonica	T. japonica	T. japonica
var. typica	var. japonica	var. japonica	f. japonica
f. vulgaris	var. glabrata	var. formosa	f. formosa
f. viridescens	(var. formosa)	(var. glabrata)	(var. glabrata)
var. glabrata	var. musashiensis	(var. musashiensis)	(f. viridescens)
(var. formosa)	(f. viridescens)	f. viridescens	T. musashiensis

a) This infraspecific treatment is the same as that of Shing *et al.* (1999), although they used the genus *Parathelypteris* instead of *Thelypteris*. Var. *musashiensis* Hiyama (1951) was not known by Ito (1939).

b) Nakaike (1992) adopted the same infraspecific treatment under the genus *Parathelypteris*.

Löve & D. Löve, Taxon 26: 325, 1977. Type: *Blomfield s.n.*, Nagasaki, Kyushu, Japan (κ).

1-1. Forma **japonica** (Fig. 2C)

Distribution: Japan (widely distributed in Honshu, Shikoku and Kyushu; Kurata & Nakaike 1983), Korea (central and southern Korea, precise range uncertain), China (Jiangsu, Jiangxi, Fujian, Guizhou, Sichuan, Taiwan?; Shing *et al.* 1999).

Japanese name: Harigane-warabi (Harigane-shida).

1-2. Forma **formosa** (C. Chr.) Nakato, Sahashi & M.Kato, **stat. nov.** (Figs. 2D & 9A)

Dryopteris formosa Nakai, Bot. Mag. Tokyo 45: 97, 1931, non Maxon 1909, 1920 — *Dryopteris japonica* var. *formosa* C. Chr., Ind. Fil. Suppl. III. 86, 1934 — *Thelypteris japonica* var. *formosa* (C. Chr.) Nakaike, Enum. Pterid. Jap. 300, 1975, p.p.; Kurata & Nakaike, Ill. Pterid. Jap. 3: 604, 1983, p.p. — *Wagneriopteris formosa* (C. Chr.) Á. Löve & D. Löve, Taxon 26: 325, 1977 — *Parathelypteris japonica* var. *formosa* (C. Chr.) Nakaike, New Fl. Jap., Rev. & enlarg. ed. 565, 1992, p.p. Type: Nakai 13259, Kôryô, Prov. Keiki, Korea (TI!); Paratype, Uchiyama *s.n.*, Namsan, Prov. Keiki, Korea, pro syn. (TI!).

Thelypteris japonica var. *glabrata* Ching, Bull. Fan Mem. Inst. Biol. 6: 313, 1936; H.Ito, in Nakai & Honda, Nov. Fl. Jap. 4: 136, 1939; Iwatsuki, Mem.

Coll. Sci. Univ. Kyoto, B, 31: 165, 1965; Ferns & Fern Allies Jap. 215, 1992; in Iwatsuki *et al.* (eds.) Fl. Jap. 1: 186, 1995; Sugimoto, Keys Herb. Pl. Jap. Pterid. 330, 1966 — *Parathelypteris japonica* var. *glabrata* (Ching) Shing, Fl. Jiangxi 1: 201, 1993; Shing *et al.* Fl. Reipubl. Popularis Sin. 4: 53, 1999 — *Lastrea japonica* var. *glabrata* (Ching) Ohwi, Fl. Jap. Pterid. 98, 1957. Type: *Faurie 27* partim, Quelapaert Isl., Korea (herbarium uncertain¹⁾).

Dryopteris japonica var. *viridescens* Makino, Genshoku Yagai Shokubutu Zufu 225, 1933 — *Thelypteris japonica* f. *viridescens* H. Ito, in Nakai & Honda, Nova Fl. Jap. Polypod.-Dryopt. I. 135, 1939; Nakaike, Enum. Pterid. Jap. 300, 1975. as synonym.

Thelypteris japonica var. *musashiensis* sensu Iwatsuki, Mem. Coll. Sci. Univ. Kyoto, B, 31: 165, 1965, p.p. excl. basion.; Ferns & Fern Allies Jap. 215, 1992, p.p. excl. basion.; in Iwatsuki *et al.* (eds.) Fl. Jap. 1: 186, 1995, p.p. excl. basion. — *Lastrea japonica* var. *musashiensis* sensu Honda, Nom. Pl. Jap. ed. emend. 379, 1957, p.p. excl. basion.; Tagawa, Col. Ill. Jap. Pterid. 110, 1959, p.p. excl. basion. — *Parathelypteris japonica* var. *musashiensis* sensu Jiang ex Shing *et al.*, Fl. Reipubl. Popularis Sin. 4: 53, 1999, p.p. excl. basion.

Distribution: Japan (Honshu: Akita, Miyagi, Ibaraki, Gunma, Chiba, Tokyo, Nagano, Toyama, Mie, Nara, Hyogo; probably more widely distributed

in Honshu, and also Shikoku and Kyushu), Korea (Jeju Isl.; Gyeonggi-Do, Gwangneung; Chungcheongbuk-Do, Mt. Sognisan), probably China.

Japanese name: Ao-harigane-warabi (Makino 1933; Kôrai-yawara-shida [Nakai 1931], Shirojiku-harigane-warabi [Sugimoto 1966]).

Note: As to Chinese material, Shing *et al.* (1999) cited a locality, Jiangxi (Lu Shan). However, identification should be verified by chromosome counts or spore observations.

2. *Thelypteris musashiensis* (Hiyama) Nakato, Sahashi & M.Kato, *stat. nov.* (Figs. 2A, B & 9B)

Thelypteris japonica var. *musashiensis* Hiyama, J. Jpn. Bot. 26: 155, 1951; Iwatsuki, Mem. Coll. Sci. Univ. Kyoto, B, 31: 163, 1965, p.p.; Fern & Fern Allies Jap., 215, 1992, p.p.; in Iwatsuki *et al.* (eds.) Fl. Jap. 1: 186, 1995, p.p. — *Lastrea japonica* var. *musashiensis* (Hiyama) Honda in Nom. Pl. Jap. ed. emend. 379, 1957, p.p.; Tagawa, Col. Ill. Jap. Pterid. 110, 1959, p.p. — *Parathelypteris japonica* var. *musashiensis* (Hiyama) Jiang ex Shing *et al.*, Fl. Reipubl. Popularis Sin. 4: 53, 1999, p.p. Type: *Hiyama s.n.*, Jul. 27, 1948, Mt. Bôno-ore, Prov. Musashi, Japan (TNS!).

Distribution: Japan (Honshu: Akita, Gunma, Tochigi, Saitama, Tokyo, Nagano, Toyama, Shiga, Kyoto, Wakayama, Osaka, Hyogo, Tottori. Shikoku: Tokushima; probably more widely distributed in Honshu, Shikoku and also Kyushu), Korea (Jeollabuku-Do, Mt. Deokyusan; Gyeongsangnam-Do, Mt. Jirisan; Gyeongsanbuk-Do, Mt. Palgongsan), probably China.

Japanese name: Iwa-harigane-warabi (Hiyama 1951).

Note: The distribution of Japanese *Thelypteris japonica* var. *formosa* sensu Nakaike (= *T. musashiensis* in the present study) was compiled by Kurata & Nakaike (1983). As to Chinese plants, Shing *et al.* (1999) cited the following localities of var. *musashiensis*: Anhui, Zhejiang, Jiangxi, Fujian, Hunan and Yunnan. However, the specimens treat-

ed in these studies may include *T. japonica* f. *formosa* (4x) or the hybrid (3x) described below.

3. *Thelypteris japonica* (Baker) Ching × *T. musashiensis* (Hiyama) Nakato, Sahashi & M.Kato (Figs. 2E, F)

This is a triploid hybrid between *Thelypteris japonica* (4x) and *T. musashiensis* (2x). It is probably sterile with abortive spores and morphologically similar to both parents and intermediate between them. Because the hybrid has both castaneous and stramineous stipes, it is likely that both f. *japonica* and f. *formosa* are involved in the hybridization.

Specimens examined: listed in Table 1 and Appendix.

Distribution: Japan (Honshu: Fukushima, Gunma, Tokyo, Chiba, Nagano; probably more widely distributed in Honshu, and also Shikoku and Kyushu), Korea (Gyeongsangnam-Do, Mt. Jirisan), probably China.

Japanese name: Ai-harigane-warabi (proposed here).

Endnote

1): Ching (1936) did not cite the herbarium where the type of var. *glabrata* was deposited, though he stated in the introduction of the paper that his studies used mainly herbarium specimens loaned from Riksmuseum Herbarium, Stockholm, the United States National Herbarium, Washington, D.C., and the Herbarium of Rosenstock.

2): Triploid and tetraploid chromosome numbers were erroneously recorded for var. *musashiensis* in Takamiya's Index (1996), and all of these must be replaced to var. *japonica*.

We thank T. Nakaike for his nomenclatural suggestion, and the directors and curators of KYO, MAK, TI, TKB and TNS for permission to examine specimens.

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Appendix

Herbarium specimens with stramineous stipes classified by perispores. Figures in parentheses after herbarium codes indicate the length and width (cm) of the largest fertile pinna.

1. Echinate perispore (*Thelypteris musashiensis*)

KOREA: Zenhoku, Chosui-gun, Mt. Tokuyu (Jeollabuku-Do, Mt. Deokysan) *Cho* 586, TNS (9.5, 2.2) & KYO (10.3, 2.0); Mt. Tii (Gyeongsangnam-Do, Mt. Jirisan), ca. 900 m, *Okamoto* 19063, TNS (7.9, 1.2) & KYO (7.8, 1.8), Fig. 7C, D; Keihoku, Mt. Hachiko (Gyeongsangbuk-Do, Mt. Palgongsan), *Oh* TKB 42099 (11.1, 2.0).

JAPAN: Pref. Akita, Mt. Tashiro-dake, *Matsuda* 16, TI (5.0, 1.1); Prov. Kozuke (Pref. Gunma), Maehotaka, Kawaba-mura, *Kurata s.n.* Aug. 21, 1975, TNS (10.0, 2.0); Pref. Tochigi, Chuzenji-Hangetsu pass, *Tagawa & Iwatsuki* 1829, KYO (9.0, 1.4); Prov. Shimotuke (Pref. Tochigi), Shimotsuga-gun, Itaga, Mt. Kawabakeyama, *Maekawa* 80216, TI (10.0, 1.8); Prov. Musashi (Pref. Saitama), Mt. Izuga-take, *Okuyama s.n.*, Jul. 7, 1935, TI (6.0, 1.4); Pref. Saitama, Hanno-shi, Higashiagano, *Nakaike s.n.* Sept. 28, 1975, TNS (3.8, 0.8); Prov. Shinano (Pref. Nagano), Nakafusa-Ariake, *Momose s.n.*, Aug. 15, 1933, TI (7.2, 1.5); Prov. Shinano (Pref. Nagano), Ariake-mura, *Hiratsuka* 113, TI (7.3, 1.2); Pref. Nagano, Saku-shi, Kabuto-iwa, *Nakayama* 35, TNS (7.8, 1.8); Pref. Toyama, Kurobe-kyokoku, *Ito* TKB 42107 (10.3, 2.0); Pref. Shiga, Shiga-cho, Mt. Uchimi, *Yahara* 4054, TNS (11.1, 2.7); Prov. Oumi (Pref. Shiga), *Makino s.n.*, 1917, MAK 140600 (10.5, 1.9); Pref. Kyoto, Kitakuwata-gun, Miyama-cho, *Mitsuta* 1481, KYO (7.2, 1.2); Ohdaigahara-sanroku, *Sacaguchi s.n.*, 1929.9, TI (6.5, 1.9); Pref. Wakayama, Arita-gun, Ohtani in Wakayama experimental forest of

Kyoto Univ., *Tagawa & Iwatsuki* 381, KYO (6.5, 1.3); Pref. Osaka, Mt. Iwawaki, *Tagawa* 3437, KYO (8.6, 1.9); Pref. Hyogo, Mt. Myoko, Hikami-gun, *Tagawa* 6425, KYO (12.0, 1.6); Pref. Tottori, Mt. Mikuni-yama, *Tanaka s.n.*, Aug. 13, 1958, KYO (8.3, 1.3); Prov. Awa (Pref. Tokushima), Myozai-gun, Kamiyama, *Inobu* TKB 42090 (10.4, 2.0); Pref. Tokushima, Myozai-gun, Jinryo-son, *Inobu* 10, TI (8.4, 1.8).

2. Membranous perispore (*T. japonica* f. *formosa*)

KOREA: Prov. Keiki, Kôryô (Gyeonggi-Do, Gwangneung), *Nakai* 13259 (Type of *Dryopteris formosa* Nakai 1931, non Maxon 1909, Fig. 7A, B), TI (6.2, 1.3); Chuhoku, Zokuri-san (Chungcheongbuk-Do, Mt. Songnisan), *Nakai* 14860, TI (9.7, 1.6).

JAPAN: Prov. Ugo (Pref. Akita), Mt. Nyutosan, *Kobayashi* 6, TI (8.7, 1.8); Prov. Rikuzen (Pref. Miyagi), Sendai, *Iishiba s.n.*, Sep. 28, 1912, KYO (7.4, 1.1); Prov. Hitachi (Pref. Ibaraki), Higashiibaraki-gun, Midorigaokamura, *Tsurumachi s.n.*, Oct. 26, 1936, KYO (12.0, 2.0), and *Tsurumachi s.n.*, Nov. 11, 1936, KYO (9.5, 1.5); Pref. Gunma, Kozu-bokujo, *Satomi* TKB 42087 (8.3, 1.4); (Pref. Chiba), Matsudo, *Makino s.n.*, 1909, MAK 113515 (10.5, 1.7); Shinshu (Pref. Nagano), Ina-gun, Ohshima-machi, Sakurayama, *Muramatsu* 1304, TNS (7.3, 1.3); Pref. Toyama, Tonami-shi, Seridani-machi, *Ohshima* TNS 343915 (11.5, 1.8); Prov. Ise (Pref. Mie), Ujiyamada, *Magofuku* 5, TI (9.6, 1.6); Pref. Nara, Mt. Kasuga, *Tagawa* 4217, TNS (8.6, 1.9) & KYO (8.6, 1.6); Pref. Hyogo, Kasai-gun, Hokkesan, *Kodama* 3644, TNS (10.2, 1.9).

3. Abortive spores (*T. japonica* × *T. musashiensis*)

KOREA: Zennan, Chiisan (Gyeongsangnam-Do, Mt. Jirisan), *Housawa* 85136, TNS (7.8, 1.4).

JAPAN: Pref. Fukushima, Ishikawa-gun, *Umemura* 256, TI (8.7, 1.3); Pref. Gunma, Mt. Arafune, *Satomi* TKB 42082 (8.5, 1.5); Pref. Chiba, Ichikawa-shi, Omachi, *H. Ohba* 626902, TI (10.5, 1.8); Prov. Shimousa (Pref. Chiba), Funabashi-shi, Komuro-machi, *H. Ohba* 1975, TI (14.8, 2.7); Pref. Nagano, Nobeyama, *K. Sato* 402, TI (8.6, 1.7); Pref. Nagano, Saku-shi, Mt. Kabuto-iwa, *Nakayama* 34, TNS (9.2, 1.9).

Received March 27, 2004 ; accepted April 19, 2004